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Incisor Microwear, Diet, and Tooth Use in Three Amerindian Populations

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ABSTRACT Incisor microwear patterns have been shown to reflect aspects of diet and ingestive behaviors in a wide range of nonhuman primates. While some studies have suggested that anterior dental microwear might be used to infer unusual front tooth use practices in archaeological populations, quantitative work on modern human incisors has thus far been limited. In this study we examined dental microwear on the maxillary central incisors of three groups of humans: Aleutian Islanders (n = 16), Arikara from the Mobridge Site in South Dakota (n = 15), and a Late Woodland Bluff sample from Jersey County, Illinois (n = 17). High-resolution replicas were prepared and examined by scanning electron microscopy following conventional procedures. Photomicrographs were taken at consistent locations on the labial surface, and microwear was quantified using Microware 3.0 (Ungar, 1997). Statistical test results revealed significant differences among the groups in microwear feature densities, sizes, and shapes. The Aleut, Arikara, and Illinois Bluff samples showed a gradient of increasing microwear density, increasing linearity in feature shape, and decreasing feature size. These differences evidently correspond to amount of meat consumption, and apparently to degree of use of the incisors in heavy loading. No differences were observed between groups in heterogeneity of feature orientations, and no sex-related differences were found. Associations between incisor microwear on the one hand and subsistence practice and anterior tooth use on the other likely have important implications for the study of hominid paleobiology. Am J Phys Anthropol 109:387–396, 1999.

Incisor microwear patterns have been suggested to reflect the diets and ingestive behaviors of nonhuman primates and the subsistence practices and anterior tooth use behaviors of human populations. Such studies have considerable implications for our understanding of the paleobiology of fossil hominids and other extinct primates. As but one example, researchers have suggested on the basis of incisor wear patterns (and other things, such as incisor size and shape, and craniofacial form) that Neandertals used their front teeth extensively for a variety of activities, including the preparation of animal hides. While some of this research (e.g., Ryan, 1980, 1993) has been grounded in studies of modern humans, further comparative work will likely lead to new insights into the subsistence practices and anterior tooth use behaviors of our hominid forebears.

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This study presents an examination of incisor microwear of three bioarchaeological populations (Aleut, Arikara, and Illinois Bluff peoples), with an eye toward the interpretation of anterior tooth wear in fossil hominids. Data presented here suggest that incisor microwear patterns do indeed reflect differences in subsistence and inferred anterior tooth use behaviors.

The Aleut, Arikara, and Illinois Bluff samples show a gradient of increasing microwear density, increasing linearity in feature shape, and decreasing feature size. These differences evidently correspond to amount of meat consumption, and to degree of use of the incisors in heavy loading. These results suggest that incisor microwear has the potential to help reveal important information about subsistence practices and anterior tooth use behaviors in early hominids and other fossil primates.

BACKGROUND

Incisor microwear has been examined for a wide variety of mammals, including such disparate groups as the Canadian moose (Young and Marty, 1986) and the Australian kangaroo (Young et al., 1987). Still, most such studies have been conducted on the anterior teeth of primates (Walker, 1976; Jacobs, 1981; Rose et al., 1981; Ryan, 1981, 1993; Teaford, 1983; Kelley, 1986, 1990; Ungar, 1990, 1994). These analyses suggest that incisor microwear patterns reflect aspects of diet as well as ingestion and other facets of anterior tooth use in predictable ways.

For example, strepsirhine anterior dental microwear studies have associated fine vertical grooves with hairs contacting the mesial and distal sides of the lower incisors during grooming (Rose et al., 1981). Such evidence of grooming has been found on Miocene lorisoid (*Nyctoceboides*) and Eocene omomyoid (*Necrolemur, Microchoerus*) incisors (Jacobs, 1981; Schmid, 1983), and may be of direct relevance to arguments concerning the origins of the tooth comb in the strepsirhines.

Further, studies of anthropoid primate anterior teeth have suggested that incisor microwear can reveal information about aspects of diet, ingestive behaviors, and perhaps even feeding height in the canopy (or on the ground). For example, Kelley (1990) reasoned, based on observations of colobus monkeys, that those primates that make use of their incisors to process items such as seeds for ingestion should have higher densities of microwear on their incisors than those that do not. The data of Ungar (1990, 1994) on Venezuelan platyrrhines and Sumatran catarrhines lend support to the association between degree of incisor use and microwear feature density. Ryan (1980, 1981) argued that specific behaviors, such as leaf-stripping by gorillas and seed-crushing by baboons, would leave characteristic striations and pitting on incisor surfaces, and Walker (1976), Teaford (1983), and Ungar (1994) all argued that incisor microwear striation orientations might provide further evidence of specific aspects of ingestive behavior. Finally, incisor microwear has even been suggested to give us some clues regarding substrate use, as Walker (1976) found higher densities of microwear striations in incisor dentine for terrestrial than for arboreal cercopithecines. Likewise, Ungar (1994, 1998) noted that arboreal forest primates tend to have broader striations on average than do more terrestrial forms, evidently related to differences in the sizes and shapes of abrasives.

Some studies have also examined incisor microwear in modern human groups (e.g., Ryan, 1980; Lukacs and Pastor, 1987; Bullington, 1991). Lukacs and Pastor (1987), for example, suggested that maxillary incisor microwear in bioarchaeological populations might result from cultural activities such as wearing lip plugs or labrets, retouching stone tools, the “stuff and cut” method of eating meat, grasping the mouthpiece or bit of a bow drill, or splitting reed and bamboo stalks. Ryan (1980, 1993) further attributed extensive wear and large, prominent gouges on Inuit incisors (and to a lesser extent those of other groups) to hide processing and other cultural activities, and suggested that similar patterns on Neandertal teeth indicate paramasticatory power-grasping activities.

MATERIALS AND METHODS

The population

The study presented here provides further evidence for the association of incisor mi-

crowear patterns with subsistence practices and inferred anterior tooth use behaviors of modern humans. Maxillary central incisors (I^1s) of specimens from the following groups were examined: 1) protohistoric Aleutian Islanders (n = 16); 2) Late Woodland peoples from the Jersey Bluff culture (n = 17), Jersey County, Illinois; and 3) Arikara peoples (n = 15) from central South Dakota (see Appendix). All specimens were housed in the collections of the Department of Anthropology at the US National Museum of Natural History (Washington, DC) at the time of study. These groups are known to differ in subsistence practices expected to affect incisor microwear patterns.

Aleut. The Aleut specimens examined for this study were collected by Hrdlička (1945) during his expeditions to Amoknak, Kagamil, Unalaska, Agatu, and Umnak Islands. Most individuals studied are protohistoric and lived after AD 1700 (McCartney, personal communication). Ethnohistorical accounts of Aleutian Islanders report an almost exclusively animal (largely marine) subsistence base, including fresh and dried fish, mollusks, and sea mammals. Their diet was only occasionally supplemented with land resources, such as edible tubers, rodents, and foxes (Hrdlička, 1945; Laughlin, 1963).

Merbs (1968) noted that the Aleut ethnographic literature indicates that these peoples used their anterior teeth as a "third hand," much as has been reported for the Inuit (De Poncins, 1941; Oswalt, 1967) and other peoples. For example, the earliest accounts demonstrate the importance of "stuff-and-cut" behavior, in which a knife is used to cut food items held between the front teeth (Brace, 1975). Indeed, Chirikov's account of first contact in 1741 describes a trade wherein the protohistoric Aleut gestured for knives, showing the manner in which they ate meat, "cutting off a portion suitable for chewing in front of one's lips" (Black, 1984). Of particular interest is the habitual use of the anterior dentition for ingesting tough, dried meat, which undoubtedly led to repetitive and probably high-magnitude loading. Veniaminov (1840; cited in HrdliČka, 1945) observed that "March among the Aleuts was the month when food was most scarce and for this reason was called Kisiagunak, i.e., 'when they chew straps.' "

Illinois Bluff. The Illinois Bluff specimens used in this study were collected in Jersey County, Illinois during the late 19th century and were described by Titterington (1935–1936). The sample probably dates to between AD 600–900, and is typical of the Patrick phase of the Late Woodland cultural tradition, which was characterized by a subsistence base of incipient agriculture or food-gathering, supplemented by hunting of small and nongregarious game and fish, and gathering of wild plant foods (Spencer et al., 1965; Kelly et al., 1984). Kelly and Cross (1984) detailed the diets of these peoples. Paleobotanical analyses indicate that they ate wild fruits, nuts, tubers, and berries. Domesticates included squash and march elder and, to a lesser degree, sunflowers and maize (the latter particularly after AD 800). *Chenopodium*, maygrass, and smartweed may have also been cultivated for their starchy seeds. Faunal analysis indicates that deer, rodents, shellfish, and birds were all eaten, though meat was clearly less significant to Illinois Bluff diets than to the diets of Aleut and Arikara peoples.

In contrast to that of the Aleuts, such a diet is unlikely to have been associated with particularly high-magnitude or repetitive masticatory loading of the anterior teeth: foods were cooked, and meat was a lesser component of the diet.

Arikara. Most of the Arikara specimens examined for this study were collected by Stirling from the Mobridge Site (39WW1), and evidently date to between AD 1600–1700 (see Wedel, 1955; Jantz, 1973). The Arikara (or pre-Arikara) of the Mobridge Site made ample use of both plant and animal foods. They gathered wild plants, such as black cherries, peppers, grapes, pumpkin and *Chenopodium*, and were successful horticulturalists, cultivating some maize, beans, squash, and sunflowers (Hurt, 1969; Meyer, 1977; Blakeslee, 1994; Tuross and Fogel, 1994). Still, as a Plains group they had access to and made considerable use of bison and other large game. Bison

meat was cut into strips and dried, and may have comprised up to half of the Arikara's yearly diet (Meyer, 1977). These peoples also hunted smaller game, including deer, antelope, and jackrabbit.

As with the Aleuts, the ingestion of tough, dried meat by the Arikara was probably associated with repetitive and/or high-magnitude masticatory loading on the incisors. It is likely, therefore, that the Arikara were intermediate between the Illinois Bluff and Aleut populations in quantity of meat consumed and in the mechanical demands placed on their front teeth.

Methods of analysis

Specimens were prepared following usual microwear procedures. First, maxillary central incisors (I^1s) were cleaned gently with cotton swabs soaked with acetone and alcohol. Molds were taken with a hydrophobic polyvinylsiloxane (Coltène President's Jet, regular body, Mawah, NJ) impression material. Replicas were poured using Epotek 301 resin and hardener (Top Plastics, Inc., Dublin, CA). Hardened casts were mounted on aluminum Cambridge scanning electron microscope (SEM) stubs with glyptal (a lacquer cement) and colloidal graphite (to ensure conductivity), and sputter-coated with approximately 20 nm of gold.

Specimens were then were examined by scanning electron microscopy. I^1s were imaged in secondary mode at 500× using a Hitachi 52300 SEM operating with a tungsten filament and an accelerating voltage of 15 keV. Photomicrographs of labial surfaces were taken at a consistent location just beyond the incisal edge, along or near the midsagittal plane (Fig. 1). All surfaces examined were oriented nearly perpendicular to the electron beam to minimize feature foreshortening (see Gordon, 1988 for discussion).

A 3.2 × 2.4 inch portion of each photomicrograph was scanned at 200 dpi resolution with 256 levels of grey (resulting in a 640 × 480 pixel image), using a flatbed image scanner. Resulting images were then displayed on a 20-inch monitor in sVGA-3 (1,280 × 1,024) mode, for an effective magnification of 1,200×, a resolution of 0.254µm per pixel, and a total of 0.02 mm^2 of tooth surface area sampled. Images were analyzed using Microware 3.0 (Ungar, 1997) in a Windows 95 (Microsoft Corp., Redmond, WA) operating environment. A mouse-driven pointer was used to define four points for each microwear feature: two each to identify the endpoints of the major and minor axes (or lengths and widths). Data were analyzed using Systat 7.0 (SPSS, Inc., Chicago, IL).

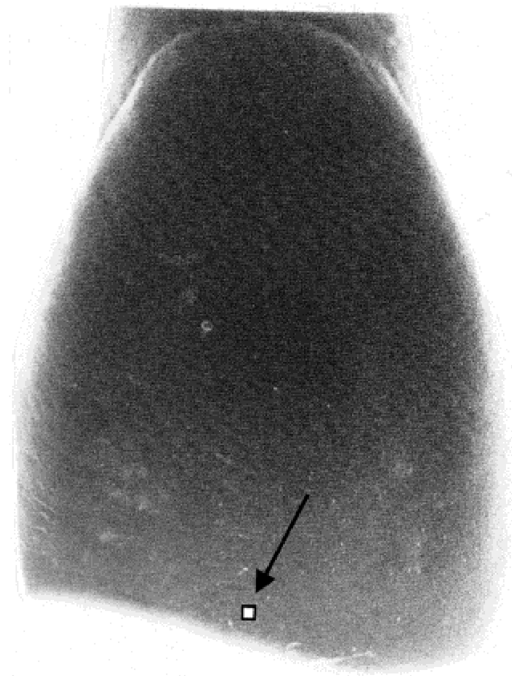

Fig. 1. Area sampled in this study.

The following data were analyzed: 1) feature density (i.e., counts per image); 2) mean feature length per micrograph; 3) mean feature breadth per micrograph; 4) average feature shape (length/width × 100); and 5) feature long-axis orientation vector length (r) for each micrograph (a measure of feature orientation homogeneity; see Ungar, 1994). Data were rank-transformed (Conover and Iman, 1981) and analyzed using a multivariate analysis of variance (MANOVA) to determine whether groups differed in overall microwear patterns. Analyses of variance for each variable and Tukey honestly significant difference (HSD) multiple comparisons tests were used to determine the sources of significant variation. Further, a two-factor

TABLE 1. Summary statistics[1]

	Aleut		Arikara		Illinois Bluff	
	Mean	SD	Mean	SD	Mean	SD
Width	2.07	0.480	1.54	0.192	1.38	0.233
Length	38.77	5.673	39.15	4.880	35.12	3.942
Shape	25.06	4.268	31.83	5.388	33.67	7.193
r	0.58	0.145	0.69	0.119	0.65	0.137

[1] Width and length values are in microns.

TABLE 2. Multivariate analysis of variance test results (mixed sex sample)[1]

A. Wilks' lambda = 0.291
   F-statistic = 7.007, df = 10, 82, P = 0.000
B. Pillai trace = 0.832
   F-statistic = 5.981, df = 10, 84, P = 0.000
C. Hotelling-Lawley trace = 2.018
   F-statistic = 8.071, df = 10, 80, P = 0.000

[1] Variables considered include feature width, length, shape, long-axis orientation concentration, and density. This analysis was conducted on rank-transformed data.

TABLE 3. Univariate F-tests (mixed sex sample)[1]

Effect	SS	df	MS	F	*P*
Feature length	1,281.545	2	640.772	3.636	0.034
Error	7,930.455	45	176.232		
Feature width	4,325.033	2	2,162.517	19.915	0.000
Error	4,886.467	45	108.588		
Feature density	4,998.840	2	2,499.420	26.702	0.000
Error	4,212.160	45	93.604		
Feature shape	3,098.375	2	1,549.188	11.403	0.000
Error	6,113.625	45	135.858		
Striation r	1,064.712	2	532.356	2.941	0.063
Error	8,144.288	45	180.984		

[1] This analysis was conducted on rank-transformed data.

TABLE 4. Tukey HSD multiple comparisons tests (mixed sex sample)

	Matrix of pairwise mean differences		Matrix of pairwise Tukey HSD probabilities	
	Aleut	Arikara	Aleut	Arikara
Feature length				
Arikara	1.762		0.928	
Illinois	−9.849	−11.612	0.095	0.045
Feature width				
Arikara	−15.119		0.001	
Illinois	−22.572	−7.453	0.000	0.119
Feature density				
Arikara	10.340		0.013	
Illinois	24.494	14.155	0.000	0.000
Feature shape				
Arikara	14.558		0.003	
Illinois	18.566	4.008	0.000	0.599

TABLE 5. Two-factor multivariate analysis of variance test results[1]

A. Sex effect MANOVA
   Wilks' lambda = 0.918
   F-statistic = 0.659, df = 5, 37, P = 0.656
   Pillai trace = 0.082
   F-statistic = 0.659, df = 5, 37, P = 0.656
   Hotelling-Lawley trace = 0.089
   F-statistic = 0.659, df = 5, 37, P = 0.656
B. Group × sex interaction MANOVA
   Wilks' lambda = 0.733
   F-statistic = 1.241, df = 10, 74, P = 0.280
   Pillai trace = 0.276
   F-statistic = 1.215, df = 10, 76, P = 0.295
   Hotelling-Lawley trace = 0.351
   F-statistic = 1.265, df = 10, 72, P = 0.267

[1] Factors include group and sex. Variables considered include feature width, length, shape, long-axis orientation concentration, and density. This analysis was conducted on rank-transformed data for specimens with reported sex. Sex attributions were based on museum catalog designations.

MANOVA with group and sex as factors was employed for specimens with known sex to assess possible effects of this variable on microwear patterns. A significant interaction between factors would indicate that sex differences were not consistent among the groups.

This study was restricted to permanent I^1s showing at least some gross wear, so all individuals were evidently adults or subadults. Still, age was not considered as a factor in this analysis. No data were available for age at death, and we did not feel that we could consistently estimate ages accurately using gross wear criteria because of between-group variation in dietary abrasiveness (see Rose and Ungar, 1998). Further, while some studies (Bullington, 1991; Pérez-Pérez et al., 1994) suggested age-related variation in microwear patterns within groups (particularly between juveniles and adults), significant differences are still evident between groups studied, and so should not obscure differences related to diet and tooth use in our study.

RESULTS

Results are presented in Tables 1–5 and are illustrated in Figures 2 and 3. Figure 2 shows representative micrographs for each group. Summary statistics are presented in Table 1 and Figure 3. MANOVA results indicate significant differences in microwear patterns among the groups using Wilks' lambda, Pillai trace, and Hotelling-Lawley trace statistical tests (Table 2). Individual ANOVAs indicate significant variation among the groups in microwear feature lengths, widths, densities, and shapes, but

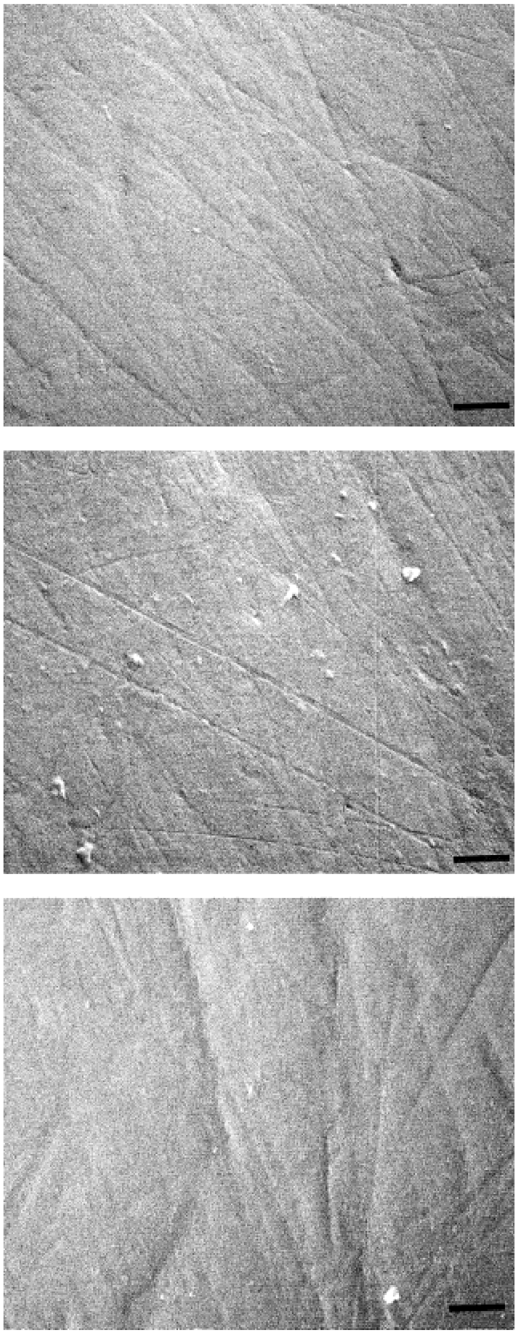

Fig. 2. Photomicrographs of representative I^1 labial surfaces of Illinois Bluff (**top**), Arikara (**middle**), and Aleut (**bottom**) specimens. Scale bars, 25µm.

not feature orientation homogeneity (Table 3). Multiple comparisons tests (Table 4) on those attributes that show significant variation indicate that the Aleut have significantly broader features than the Illinois Bluff specimens. The Aleut also have features with lower length-to-width ratios and overall lower feature densities than the Illinois Bluff specimens. The Arikara are intermediate in most of these attributes, with significantly higher microwear feature densities, narrower features, and higher feature length-to-width ratios than the Aleut. The Arikara also have significantly longer microwear features and lower densities of features than the Illinois Bluff specimens. In summary, the general trend indicates a gradient toward lower densities of larger, less linear features from Illinois Bluff to Arikara to Aleut samples. Finally, MANOVA results showed no significant sex effect in microwear patterning for the groups studied, nor was there a significant interaction between sex and group that might suggest sex-related differences in microwear for some of the groups (Table 5).

DISCUSSION

Results presented here show significant differences between the groups in microwear feature densities, sizes, and shapes. Further, they indicate a gradation of microwear patterning from Illinois Bluff to Arikara to Aleut samples. Illinois Bluff specimens show higher densities of smaller, more linear features than the Aleut. The Arikara sample is intermediate for most attributes examined. This gradient corresponds nicely to reported differences in subsistence among these groups and to inferred anterior tooth use practices. At one end of the spectrum lie the Aleut, with a diet composed almost entirely of animal foods, and who must have used their incisors extensively to process hides and dried, occasionally frozen meat. At the other end of this spectrum are the Illinois Bluff peoples, who lived off of gathered and farmed plant resources and some animal foods. Intermediate between these two are the Arikara, agriculturalists who relied heavily on dried bison meat.

So, how can we explain the incisor microwear patterning given reported subsistence practices? We may be able to get some clues from studies of buccal surface molar microwear conducted by Lalueza et al. (1993), who studied six modern human groups that varied widely in meat consump-

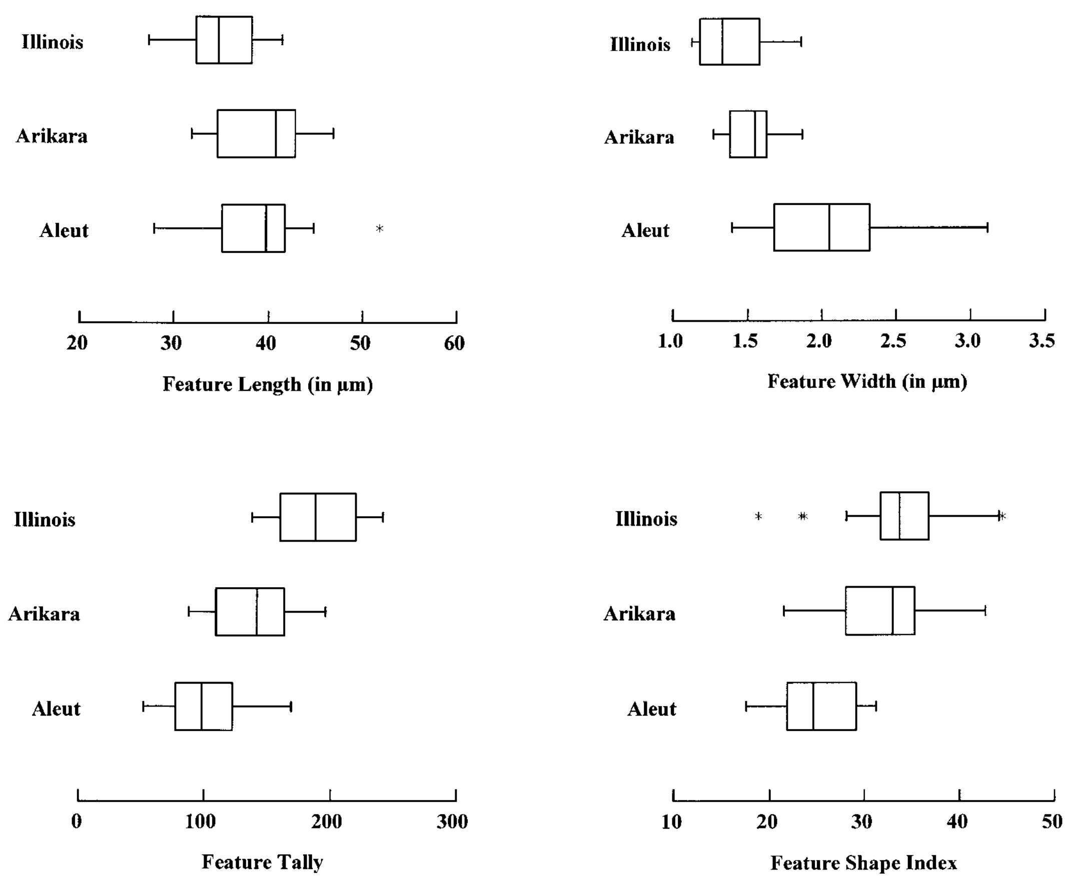

Fig. 3. Microwear feature data comparisons (upper left, feature lengths; upper right, feature widths; lower left, feature density; lower right, feature shape indices). Vertical lines within boxes indicate sample medians, box hinges represent the first and third quantiles (the central 50% of values fall within the range of the box), and whiskers or horizontal lines show values within 1.5 times the range represented by each box . Values outside this range are plotted as asterisks (after Wilkinson, 1997).

tion. Their results indicated that those peoples who ate more meat had fewer striations than those who did not. This is consistent with the idea that plant foods are more abrasive than meat. Two main causal agents have been identified for microwear formation: exogenous grit on foods, and siliceous opal phytoliths in plants (Lucas and Teaford, 1995; Ungar et al., 1995). Meat does not contain endogenous silicates, and is likely to cause microwear only when abrasive grit is adherent. Many plant foods, on the other hand, do contain endogenous silicates, and further, are likely to have abrasives added during food preparation. It therefore follows that lower feature densities on Aleut incisors compared with Arikara, and on Arikara incisors compared with Illinois Bluff, are probably due, at least in part, to ratios of meat to plant foods in the diet.

Feature sizes and shapes, on the other hand, may well relate to the intensity of forces generated during front tooth use. The data of Teaford (1988) demonstrate that hard-object feeders have wider microwear pits and scratches than those that prefer softer fruits and leaves. This suggests that feature size may relate to occlusal force, given that harder foods require larger forces during chewing than softer ones (but see Maas, 1994 for an alternative view). Further, Ryan (1980, 1993) argued that large gouges on Inuit incisors reflect “power grasping/pulling” activities such as hide preparation, or harness tightening. While the microwear features observed in this study

tended to be smaller than those reported by Ryan (1980, 1993) (he used lower magnifications in his study), the idea that broader features may be associated with powerful incisor loading might still help explain the feature size and shape differences reported here. If so, the Aleut have wider features at least in part because of forceful incisor loading.

This hypothesis gains further support from our recent study on the craniofacial biomechanics of these same groups (Spencer and Ungar, 1997). We reported that the Aleut sample differed from the other groups in several aspects of masticatory system configuration that would have allowed incisal bite forces to be produced more efficiently. Similar, though less marked features characterize the Arikara sample. Such differences in form could result from the need to produce forces repetitively as opposed to forcefully. However, coupled with estimates of the force-producing potential of the temporalis muscle, they indicate that the Aleut, and to a lesser degree the Arikara, were capable of generating relatively high-magnitude forces on their incisors. The microwear data presented here are consistent with this scenario, and suggest that these peoples may have made use of these differences in capabilities.

There are several possible explanations for the lack of significant sex differences within these groups. First, it may be that these men and women had similar diets and loading regimes in incisor use. Alternatively, perhaps the small sample sizes for females (e.g., only four females in the Aleut sample) were not sufficient to discern differences. Substantial variation in tooth use among individuals could also then swamp between-sex differences. Another possibility is that some of the sex designations used in this study are incorrect. It can be difficult to identify females when populations as a whole tend to have robust crania. Perhaps this explains why our randomly chosen sample has twice the number of identified men as women. Finally, perhaps the current technique is not sensitive enough to pick up subtle differences between the sexes. Still, at least one incisor microwear study has identified between-sex differences. In that case, male orangutans had narrower microwear striations than did females, evidently reflecting differences in sizes and shapes of abrasives associated with terrestrial as opposed to arboreal foods (Ungar, 1994). Larger samples of individuals of known sex will likely help resolve this issue.

The lack of significant differences in feature long-axis orientation concentration is also not surprising. Bax and Ungar (1999) recently found similar results for these groups in a study of labial face striation orientations visible at much lower (56×) magnification. These authors argued that striation orientation heterogeneity is not a good predictor of subsistence practices for these groups. This also seems to be the case for features observed at higher magnifications. Still, microwear feature orientation heterogeneity may be a useful indicator of subsistence practices in some cases, as Teaford et al. (1997) recently found a significant difference in this attribute between Late Prehistoric and Early Mission Amerindian populations from the Southeastern United States.

In summary, the Aleut, Arikara, and Illinois Bluff samples show a gradient of increasing microwear density, increasing linearity in feature shape, and decreasing feature size. These differences correspond to amount of meat consumption, and evidently to degree of use of the incisors in heavy loading. These results have important implications for the study of paleobiology. Incisor microwear, especially when considered with other lines of evidence such as craniofacial biomechanics, may have the potential to reveal important information about subsistence practices and anterior tooth use behaviors in early hominids and other fossil primates.

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APPENDIX. Specimens used in this study, all from the National Museum of Natural History, Washington, DC

Aleut	Arikara	Illinois Bluff
NMNH 377752	NMNH 325373	NMNH 379763
NMNH 377817	NMNH 325375	NMNH 379776
NMNH 377838	NMNH 325379	NMNH 379780
NMNH 377851	NMNH 325383	NMNH 379781
NMNH 377906	NMNH 325384	NMNH 379785
NMNH 377908	NMNH 325385	NMNH 379788
NMNH 377913	NMNH 325398	NMNH 379797
NMNH 377919	NMNH 325404	NMNH 379817
NMNH 378302	NMNH 325407	NMNH 379818
NMNH 378369	NMNH 325417	NMNH 379829
NMNH 378474	NMNH 325418	NMNH 379831
NMNH 378477	NMNH 325420	NMNH 379838
NMNH 378490	NMNH 382901	NMNH 379845
NMNH 378542	NMNH 382950	NMNH 379850
NMNH 378618	NMNH 382951	NMNH 379856
NMNH 378624		NMNH 379861
		NMNH 380043

specimens in his care, and for his help with obtaining information on the samples used in this study.

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